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Onthophagus pilauco sp. nov. (Coleoptera, Scarabaeidae): evidence of beetle extinction in the Pleistocene–Holocene transition in Chilean Northern Patagonia

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Abstract

The South American Pleistocene–Holocene transition has been characterized by drastic climatic and diversity changes. These rapid changes induced one of the largest and most recent extinctions in the megafauna at the continental scale. However, examples of the extinction of small animals (e.g., insects) are scarce, and the underlying causes of the extinction have been little studied. In this work, a new extinct dung beetle species is described from a late Pleistocene sequence (~15.2 k cal yr BP) at the paleoarcheological site Pilauco, Chilean Northern Patagonia. Based on morphological characters, this fossil is considered to belong to the genus Onthophagus Latreille, 1802 and named Onthophagus pilauco sp. nov. We carried out a comprehensive revision of related groups, and we analyzed the possible mechanisms of diversification and extinction of this new species. We hypothesize that Onthophagus pilauco sp. nov. diversified as a member of the escalatus species-complex following migration processes related to the Great American Biotic Interchange (~3 Ma). The extinction of O. pilauco sp. nov. may be related to massive defaunation and climatic changes recorded in the Plesitocene-Holocene transition (12.8 k cal yr BP). This finding is the first record of this genus in Chile, and provides new evidence to support the collateral-extinction hypothesis related to the defaunation.

Keywords

Dung beetle, extinction, fossil beetles, new species, Pleistocene, South America

Materials and methods

Abbreviations

CEMT	Seção de Entomologia da Coleção Zoológica, Universidade Federal de Mato, Grosso, Cuiabá, Brazil;
CMNC	Canadian Museum of Nature, Gatineau, Quebec, Canada;
MPDO	Museo Pleistocénico de Osorno, Osorno, Chile;
MZ	Mario Zunino private collection, Asti, Italy;
MZUF	Museo di Storia Naturale dell'Università di Firenze, Florence, Italy;
NMPC	Národní Muzeum, Prague, Czech Republic.

Drawings and determination of fossil remains

e fossil beetle remains were recovered from the sediment using an adaptation of the water otation technique described by Hoganson et al. (1989) (see also Tello and Torres 2020). e remains were collected from grid 18AC, at an elevation of 384 cm in bed PB-7. e age span of this bed is ~16.0 to 14.0 k cal yr BP (Pino et al. 2020). e taxonomic placement suggested for the fossil was made after detailed examination and a comparison with multiple modern specimens of South American Onthophagus species deposited in the CEMT, CMNC, MZUF, MZ and NMPC col lections. For the taxonomic nomenclature, we followed Rossini et al. (2018a, b). Figure 1A was obtained using R software v4.0.3. Figure 2A, 2B was obtained using a scanning electron microscope (variable pressure, EVO MC10), and Fig. 2C, D was obtained using a Leica M205C camera. All gures were processed using Adobe Photoshop 2019 CC. Type material is deposited in the MPDO insect collection, Osorno, Chile.

Results

Systematic paleontology

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Family Scarabaeidae Latreille, 1802
Genus *Onthophagus* Latreille, 1802

Type species: *Onthophagus pilauco* sp. nov.
http://zoobank.org/9B203D54-E27A-432D-8AC8-ED7C33ED2F83
Fig. 2

Description. *Holotype*. Male, minor form. Clypeus sub-trapezoidal and slightly elon gated forward, with anterior margin narrowly and slightly re exed, head margin barely

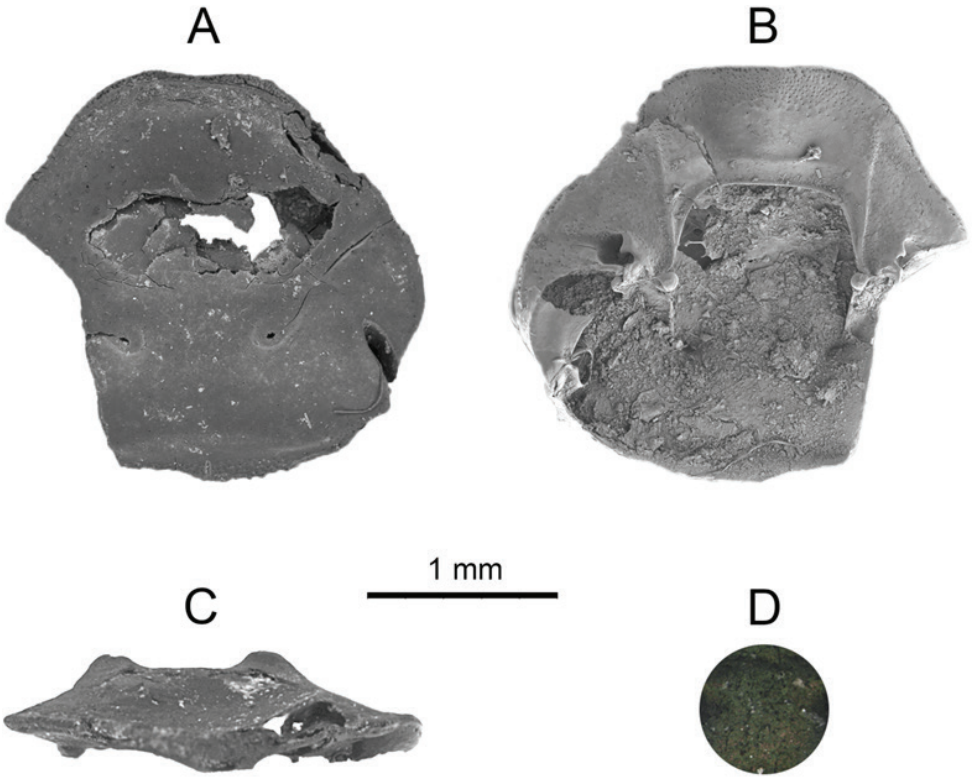

Figure 2. Holotype of *Onthophagus pilauco* sp. nov. **A** dorsal **B** ventral and **C** frontal views **D** detail of the microsculpture.

sinuated at the clypeo-genal junction. Fronto-clypeal region without carina, frons with two close, weak tubercles, strongly advanced in position, in line with the anterior margin of the eyes (Fig. 2A, C). Head surface very finely and evenly punctate. Latero-clypeal region with deeper ocellate punctures. Color dark with metallic green to bronze sheen (Fig. 2D). Pronotum and elytra not found.

Female unknown.

Diagnosis. *Onthophagus pilauco* sp. nov. is considered to be a close relative of *O. confusus* Boucomont, 1932 and *O. insularis* Boheman, 1858, as it shares the following morphological characters with these species: sub-trapezoidal shape of the clypeus; small, slightly deeper cephalic punctation, coupled with very shallow wrinkles in proximity to the genal and clypeal margins. Although the fronto-clypeal region is significantly damaged, there is no indication of a possible carina.

Proposed English and Spanish vernacular names. Pilauco dung beetle (EN) and estercolero de Pilauco (ES).

Etymology. The name of the new species refers to the archeopaleontological site from which the fossil remains were collected.

Discussion

From our observations, the fossil remains found at Pilauco correspond to a new and extinct species of the genus *Onthophagus*, closely related to the *hircus* group. *Onthophagus pilauco* sp. nov. represents the first record of an endemic species of this genus in Chile. Moreover, this record brings new evidence of beetle extinction related to the Pleistocene–Holocene transition and massive defaunation after a possible cosmic impact and/or YD cooling reversal events.

Morphological delimitation of the fossil record

Despite the beetle remains only being represented by cephalic parts (clypeus, right gena and frons; fronto-clypeal region partly damaged; left gena absent; see Fig. 2A–D), it is clear that they belong to the genus *Onthophagus*. Close scrutiny of the fossil remains, along with an extensive analysis of multiple specimens belonging to extant American *Onthophagus* led us to assign *O. pilauco* to the *O. hircus* group, and more precisely to the *escalatis* species-complex (Rossini et al. 2018a). Two cephalic horn-like tubercles may indicate that the remains belong to a male specimen, probably a minor form. The physical location of the cephalic tubercles is rather unique in the modern American *Onthophagus* fauna. They rise in a very advanced position, in line with the anterior margin of the eyes, and are quite close to each other. The combination of these two characteristics has only ever been found in an undescribed *Onthophagus* from Costa Rica, which was included in the same species group, but in a different taxonomic complex (Rossini, pers. comm. 2020). Close cephalic tubercles are also found in female specimens of species belonging to the *Onthophagus clypeatus*, *dicranius* and *mirabilis* groups, but they are always situated at the front, and never as advanced as in *O. pilauco*. Also, the shape of the clypeus in these females is always triangular or evenly curved, terminating at the apex with a margin slightly to distinctly emarginated (with two obtuse teeth).

Hypothesis for the speciation and extinction of *Onthophagus pilauco*

Comprehensive knowledge of the Chilean beetle fauna suggests that only a few species (nine) can be considered to be exclusively associated with dung resources (González-Chang and Pinochet 2015). Thus, six species have been assigned to the Scarabaeidae family (excluding the saprophagous Aphodiinae species): two species belonging to the Deltochilini tribe: *Megathopa villosa* Eschscholtz and *Scybalophagus ruginasus* (Blanchard); and four species with uncertain taxonomic position (*incertae sedis* sensu Tarasov and Dimitrov 2016): *Tesserodoniella elguetai* Vaz-de Mello & Halffter, *T. meridionalis* Vaz-de Mello & Halffter, *Homocopris punctatissimus* (Curtis), and *H. torulosus* (Eschscholtz) (González-Chang and Pinochet 2015). The placement of the genus *Homocopris* in a suprageneric group requires further research. Additionally, three dung beetle species

belong to the family Geotrupidae Latreille, 1802, represented in Chile by the subfamily Taurocerastinae: Erickius costulatus Germain, E. variolosus Germain and Taurocerastes patagonicus, which are distributed across central and southern Chile.

The Deltochilini group is distributed in the pantropical zone, being especially diversified in the northern areas of South America. The genus Tesserodoniella is related to the Australian genera Tasserodon and Aptenocanthon and their ancestors probably originated from the Gondwana supercontinent (Vaz-De-Mello and Halffter 2006). In contrast, the extant American Onthophagus is a result of migrations to the continent by intercontinental connections, the current remnants of which are known as Beringia components. These migratory processes occurred at different times and under different geographical and climatic conditions, and involved different ancestors, all belonging to the subgenus Onthophagus sensu stricto (Rossini et al. 2018a, b, Halffter et al. 2019, Zunino and Halffter 2019). Additionally, after the definitive closure of the Isthmus of Panama (~3 Ma), which eliminated natural barriers, Central America became a permanent bridge from one continent to another, improving migratory conditions for large animals and dung beetles. Therefore, we suggest that the ancestors of O. pilaucoi migrated to South America during the Great American Biotic Interchange, following large mammals at the end of the Pliocene (3 Ma). This migratory-mechanism has been suggested for the extant related group, which arrived by crossing the Andes via the Huancabamba Depression, similarly to other extinct dung beetles (e.g., Phanaeus violetae Zunino, 2013). Intra-continental migratory patterns have also been reported in extant species of dung beetles that have rapidly colonized new habitats following cattle migrations (e.g., Digitonthophagus gazella (Fabricius, 1787); see Noriega et al. 2020). Thus, ancestors of the osculatis species-complex diverged in situ in Chilean areas, resulting in the evolution of O. pilaucoi (Fig. 3). This speciation hypothesis is supported by several studies on Pleistocene Patagonian landscapes (~180 and 26 ka) that have suggested that the rapid contraction and expansion of ice cover has induced drastic changes in biotic distributions and prompted diversification in different groups of organisms (e.g., in amphibians: Nuñez et al. 2020; in mammals: Himes et al. 2008). Moreover, the presence of extant endemic species belonging to the osculatis species-complex in western Ecuador and northwestern Peru [as O. peruanus and O. insularis (Rossini et al. 2018a)] suggests that O. pilaucoi could be a species endemic to southern Chile.

On the other hand, the extinction of large animals in South American Pleistocene environments has invoked multiple climate- and human-activity-related hypotheses, and interactions between them (Barnosky et al. 2004). The causes of small animal (<60 kg) extinctions, and the implications of changes in species compositions and distributions, are poorly understood. Owen-Smith (1987) proposed the ‘keystone herbivore’ hypothesis, which provides a framework to explain the simultaneous extinctions of animals not obviously made extinct by the previous causes. Additionally, a possible cosmic impact may have generated the Younger Dryas cooling oscillation (12.8 and 11.0 k cal yr BP), resulting in a rapid defaunation process, including smaller taxa

Figure 3. Artistic reconstruction of *Onthophagus pilauco* sp. nov. and its palaeoenvironment (by Mauricio Alvarez).

(Firestone et al. 2007; Pino et al. 2019; Wolbach et al. 2020). In this case, we suggest that both the rapid climatic changes and the extensive defaunation in South America could be determining factors in the extinction of *O. pilauco* during the Pleistocene–Holocene transition.

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